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Reproductive conflicts in social animals: who has power?

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Theoretical models are often used to analyze reproductive conflicts in animal societies; for example, by determining the different sex-allocation optima of queen and workers. But who is in control (queen or workers, dominant or subordinate) is normally an implicit or explicit assumption of the model. Here, we introduce the concept of power (the ability to do or act in a situation in which conflict over reproduction exists) and argue that the relative power of conflicting individuals or groups of individuals (e.g. the workers or subordinates) within a society can complement theoretical predictions to provide a deeper understanding of reproduction in animal societies. We also show that power involves both general principles, such as differences in the quality of the information available to conflicting parties, and idiosyncrasies of the biology of different taxa, such as viviparity versus oviparity. These idiosyncrasies can occur at any taxonomic level, from a single species to an entire order or class, and are often crucial for understanding the balance of power among conflicting parties.

In many animal societies, reproduction is monopolized by one or a few individuals. Because animal societies are normally nonclonal, potential conflicts occur over which individual(s) should reproduce or which offspring should be raised [1]. Such conflicts can be formalized using inclusive fitness theory [2], with theoretical models being used to predict the optimal reproductive strategies of different individuals or parties of interest (e.g. an individual or a group of individuals that share the same interest) within the society [3,4]. However, although theory is of great importance for understanding reproductive conflicts, particularly in determining the different reproductive optima, it alone cannot explain the reproductive characteristics of a group. This is because different individuals and groups within the society often differ in their optima with respect to reproduction [5] and the theory does not say whose interest will prevail.

Who is in control of reproduction is often an implicit or explicit assumption (Box 1). For example, workers are often assumed to control the sex ratio in ants [6], adults are assumed to control the adult caste fate of immature females in bees, ants and wasps [7], and the dominant

individual in vertebrates is often assumed to control same-sex subordinate(s) at a behavioural or physiological level [8]. But how can we know which individual or party of interest is in control of reproduction in a conflict situation? Indeed, what mechanisms give one individual or party control over others?

Here, we present the concept of 'power', which we define as the ability to control reproduction when conflict exists, and discuss factors that affect power using examples from both insect and vertebrate societies. Our concept of power depends not only on the ability of one party to control reproduction, but also on the balance of the controlling abilities of all conflicting parties. We identify general principles that might play an important role in all social animals and also show that there are important idiosyncratic differences across social taxa that affect power relations. Power in itself is not a new theory, but should be seen as complementary to theoretical insights, thereby increasing our understanding of the reproductive characteristics of animal societies. In particular, better knowledge of the underlying mechanisms that determine which party or parties of interest control reproduction (i.e. their relative power) can provide information about whose interests should prevail when conflict occurs.

Power: general principles

Power over reproduction can be just a matter of sheer physical power. Dominant female naked mole-rats *Heterocephalus glaber* are the biggest and most aggressive females and their rank is achieved by fights, which often result in serious injury or death [9]. In many ants, nests are initiated by multiple foundress queens. At first, the queens share the nest peacefully, but when the first workers emerge, fighting normally occurs with the strongest female killing her rivals to take over the nest [10]. More often, however, power relations are affected by more subtle factors, such as group size, number and size of nests or dens, control over food, and information.

When groups are small, the dominant is likely to have more power, because there are fewer group members to control. But, even in large groups, the dominant might only have to exert power over a few obvious rivals, such as high rankers of its own sex. Colonies of the queenless ant *Dinoponera quadricaps* normally have ~80 females, but only a few of these are in conflict with the reigning female

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Box 1. Theoretical predictions and assumptions underlying models: why we need to consider power

Multiple optima predicted by inclusive fitness theory

Inclusive fitness theory [2] forms the basis of most models that make predictions about the outcomes of reproductive conflicts in social groups. However, theory normally indicates multiple reproductive optima, each corresponding to a different party of interest [5]. For example, consider sex allocation in ants. In a population in which each colony is headed by a single queen, randomly mated to a single male, and with all the males being the queen's sons, the workers collectively and the queen differ in their optimum sex allocation ratio because of their asymmetric relatedness (Box 3). Inclusive fitness theory tells us that the worker optimum is a 3F:1M ratio and the queen optimum is 1F:1M [6]. But the theory does not tell us whose optimum will prevail. To determine this, we need to know which party is more able to manipulate sex allocation (i.e. has more power). Although the queen determines the primary sex ratio, workers normally rear the brood and could potentially cause female bias by selectively killing males or by rearing more queens. Because the workers act after the queen, this probably gives them greater power than the queen. But if the queen can predestine female eggs to develop into workers rather than queens [38], or limit the number of female eggs [39], the workers are unable to cause greater female bias although they still rear the brood. This shows that theoretical predictions must be combined with an understanding of power, and this means considering the various mechanisms that different parties of interest have in influencing colony reproduction and how these mechanisms interact in setting the balance of power.

Assumptions underlying theoretical models

Models often sidestep the problem of who is in control by making this an assumption. The skew model of Reeve and Ratnieks [40], which investigated reproductive sharing in a group of two

breeders, assumed that the dominant female has the power to control all reproduction in the nest. Because the dominant controls the reproduction of the subordinate, the dominant can allow the subordinate a fraction of the reproduction. The only power that the subordinate has is whether to leave or stay, to fight or be peaceful. This model is then used to predict how much reproduction the dominant should allow the subordinate to make it worthwhile for her to stay, or to stay peacefully.

In tug-of-war models [41], no individual has complete control over the reproduction of the other individual and the actual levels of reproduction of the different parties depend upon the costs and benefits of exercising control. Does this mean that our concept of power is synonymous with costs and benefits? Costs do not directly affect the physical power of different parties, but are important because they determine the inclusive fitness consequences of any physical act of manipulation. A party that can only exercise power at a considerable cost to itself or the group as a whole would have little power in relation to a party that could exercise power at a low cost. A party can be considered as completely powerless when it cannot exercise any control no matter how high the costs. For example, ant workers can kill male brood to cause a female-biased sex ratio and are selected to do this even if there is less reproduction in total (i.e. total weight of young queens and males reared). But if the queen only produces male eggs during the reproductive period, killing these males will incur a great cost to the colony with no benefit to the workers because the males cannot be traded off for queens. Under more typical conditions, ant workers can presumably exert power over sex allocation at low costs. Our concept of power focuses on the mechanisms and constraints that determine whether costs of manipulative acts are high or low for particular parties of interest.

(gamergate) over reproduction, occasionally laying eggs or attempting to overthrow her [11].

Control of subordinates is likely to be affected by the number of nests or dens and the amount of time spent in the nest or den by the dominant. When all females have access to the nest, it might be impossible for one individual to have complete control over reproduction. In the acorn woodpecker *Melanerpes formicivorus*, a single female cannot defend her eggs from being eliminated by co-breeding females, and hence reproduction is more or less equal [12]. When the nest or den is large or subdivided, one party can gain power. Subordinates of African wild dogs *Lycaon pictus* often give birth in a separate den and only move their pups to the main den when they are too old to be killed by the dominant [13,14]. Having multiple nests (polydomy) is quite common in ants [15] and creates a situation in which the queen has little direct control over what goes on in the different nests because she cannot be in more than one nest at once. Weaver ants *Oecophylla* spp. are an extreme example. Here, the nest comprises many brood chambers made of leaves, and workers transport brood to these chambers for rearing. The sub-nests can be widely spread throughout the branches of a tree.

Information can also be important in power relations. Where there is asymmetry in information among parties of interest, the party with better information is likely to be the most powerful (Box 2). In addition, when there is only limited information available about kinship, manipulating reproduction is likely to be of little benefit. If you do not know who or when to help or hinder, it is better not to do anything. Thus, a party that knows who is who will be more able to manipulate the reproduction of the group at a

lower cost than will a party that does not, even if both have effectively the same general power.

Power: taxonomic idiosyncrasies

Idiosyncratic differences in the biology of a taxon can greatly affect power relations. A subordinate bird can more easily lay eggs than a subordinate mammal can give birth because egg laying is much briefer than parturition. In addition, it is probably much harder to conceal pregnancy than it is to mature an egg. Following birth, mammalian mothers lactate. Therefore, milk production could also be used as a cue to determine who reproduced, whereas such cues are not available for birds. When lactating is not restricted to the mother (as in dwarf mongoose *Helogale parvula*, where females can lactate without having been pregnant [16]) the production of milk can no longer be used to recognize reproductively active subordinates. Hence, a subordinate might breed successfully more easily. In addition to providing a cue as to who has bred, lactation can also be a means by which the breeder can direct the flow of food to young. To produce milk, a female must feed. If a subordinate were to breed, the dominant could indirectly harm her young by preventing the subordinate from feeding. In birds, all individuals can, in principle, feed young and this could reduce the dominant's power, especially when there is more than one nest.

Social Hymenoptera

Social Hymenoptera (ants, bees and wasps) have two important idiosyncrasies that affect power compared with social vertebrates. First, in most species, there is queen-worker dimorphism and, in almost all of these species, the

Box 2. Information is power

Dinoponera quadricaps is a queenless ant and, in each colony, the queen role has been taken over by a mated worker, the gamergate, who is mated to one unrelated male and is the mother of the workers. This kin structure is expected to give considerable potential conflict over male parentage. Both the offspring workers and the gamergate are more related to their own sons (0.5) than they are to sons of other individuals. Because the workers have the same father, they are more related to their nephews (0.375) than they are to their brothers (0.25) (Box 3), suggesting that worker policing will not be selected for. *Dinoponera quadricaps* workers show a linear hierarchy and, in approximately half of the colonies, the highest ranking worker, β , lays haploid eggs alongside the gamergate, α [11]. To manipulate the parentage of males, the gamergate and the β worker must discriminate between eggs laid by each other, so that they can selectively remove male eggs of the nonpreferred maternity. Information about egg maternity is available because worker- and gamergate-laid eggs are chemically distinct [42]. Yet, only the gamergate kills eggs laid by the β female whereas haploid gamergate-laid eggs are left alone by β . Why is this, given that information about egg maternity is available to all parties and all have equal access to the egg pile? The gamergate can manipulate male parentage at low cost because she knows that all eggs laid by β

are haploid. However, the killing of gamergate-laid eggs by β will also involve killing many female eggs and this will have a cost in terms of colony survival and total reproduction. Assuming that the workers cannot distinguish between the male and female eggs laid by the gamergate, this gives the gamergate greater power over male production [26], but what if β waits until the eggs have hatched and then kills the male larvae? Presumably, she can distinguish between male and female larvae but by then the larvae will have lost their maternity mark. Hence, β always lacks one piece of vital information whereas the gamergate always knows enough.

Accuracy of information also seems to determine reproductive skew in dwarf mongooses *Helogale parvula*. Dominant females are apparently able to suppress reproduction by subordinate females [43]. One important factor that affects reproductive skew is selective infanticide by the dominant female. Reproductive skew is less pronounced among males even though the dominant male would, potentially, also be able to commit infanticide and would gain as much in terms of relatedness [43]. What causes this difference? The dominant female is likely to know which offspring are hers and can therefore safely kill the offspring of a subordinate, but males are less likely to have accurate information about paternity. Hence, selective infanticide is not likely to increase the fitness of a male [44].

workers are unable to mate and produce female offspring or to replace the breeder. This means that workers might not need to be under so much control compared with vertebrate subordinates, which can mate, produce both male and female offspring, and replace a breeder of the same sex. In addition, leaving is not an option for most insect workers in species in which the queen and workers are morphologically different, whereas it is for vertebrate helpers. Second, hymenopteran societies are female societies, so we do not normally have to consider male interests. Furthermore, mating does not play a significant role in the regulation of reproduction in social Hymenoptera. Mating either does not occur at all (i.e. workers, if they reproduce, lay unfertilized, haploid eggs) or has already occurred (i.e. queens store a lifetime supply of sperm on their nuptial flight and never remate). In the rare cases in which mating is part of social life, as in the ant *Cardiocondyla* spp., there are major male–male conflicts, and the male morphs are equipped with large mandibles for fighting [17]. In social vertebrates in which the group often comprises the breeding pair and their helpers, and in termites, where both sexes are workers and the colony is headed by a queen and king, mating is part of social life and this introduces additional conflicts and power relations that are not found in social Hymenoptera.

Social vertebrates

Where there are multiple adult males within the society, conflicts over access to fertile females are likely to occur. In territorial species, such as the gorilla *Gorilla gorilla*, the dominant male controls the females within his territory and so is the only male to mate [18]. In other primates, such as baboons *Papio* spp. and chimpanzees *Pan troglodytes*, gaining access to and mating with females is a major preoccupation and subordinate males often succeed in surreptitious matings. Infanticide is a male strategy that causes nursing females to come into estrous sooner and normally follows the takeover of a group of females by a new dominant male or group of males [18].

Infanticide can also occur within the group when there are several resident males who all try to maximize their individual reproductive success. This primarily male–male conflict also involves the female because she does not normally benefit from having her nursing young killed. Hence, the female should conceal information about paternity to regain some control and which will protect her offspring from being killed. The female can either mate with several males during her fertile period or she could conceal her ovulation and mate regardless of whether she is fertile. That infanticide is not just a theoretical danger is shown by Sakamaki *et al.* [19], who describe a case in which two high-ranking chimpanzee males killed the newborn infant of a female with whom neither had mated.

Uncertainty with respect to paternity in mammals is facilitated by the fact that mating is distant in time from giving birth, thus giving females more power. In birds, mating and egg laying are less distant in time and males probably have more information about paternity, although female birds can store sperm whereas female mammals cannot. This is nicely illustrated by the polygynandrous dunnock *Prunella modularis*. Some groups comprise two males and one female, who mates with both males. Both males help provision the chicks. Dunnock males keep track of their probable paternity based on their access to the female during the fertile period, and they provision chicks more or less in proportion to mating access but not according to their actual paternity [20].

When does the collective win?

In honeybees and wasps, workers destroy eggs laid by other workers in a process known as worker policing [21–23]. Although each individual worker benefits from producing her own eggs (because she is more related to her sons than she is to any other male; Box 3), the workers collectively often do not benefit from worker reproduction because of a lower average relatedness towards worker-produced males when the queen mates to more than two males. The collective interests of the policing workers

Box 3. Unique conflict over male parentage in social Hymenoptera

Unlike vertebrates and termites, Hymenoptera (ants, bees and wasps) are haplodiploid, with males arising from unfertilized eggs. Hymenopteran queens mate with one or more males at the beginning of their lives and store the sperm from one or more males for future use. In most species, workers cannot mate but retain ovaries and are able to lay unfertilized eggs that produce sons [45]. The resulting asymmetrical relatedness within the society arising from haplodiploidy leads to unique conflicts, such as that over male parentage, where a worker can be more related to her nephew than she is to her brother (Fig. 1).

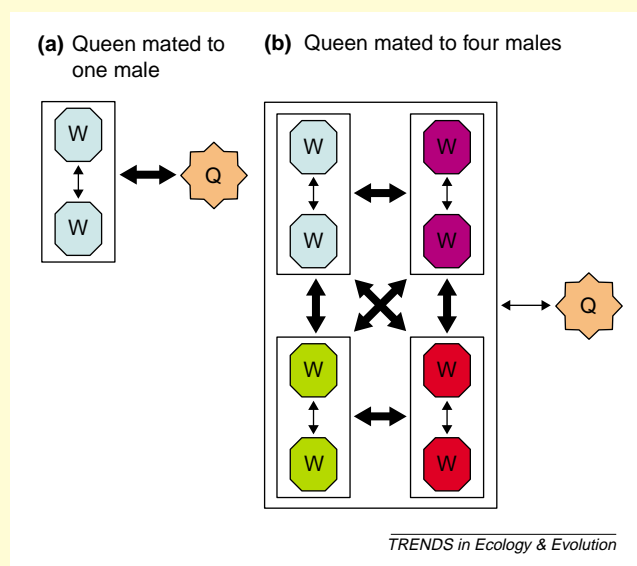


Fig. 1. Potential conflicts over male parentage in social Hymenoptera. When the queen (Q) has mated only once (a), all workers (W) are more related to the sons of workers than they are to the queen's sons. Hence, there is a strong conflict between the workers as a group and the queen, but less so among workers. Thickness of the arrows denotes the strength of the conflict. When the queen is mated to two or more males (b), workers sired by the same male (patriline) are in conflict with workers sired by a different male. Here, the conflict is mainly among the different patrilines (symbolized by different colours) and less between the workers as a group and the queen. Under these circumstances, the selective removal of worker-laid eggs by police workers, worker policing, is expected. Adapted, with permission, from [1].

prevail over individual interests, because an individual worker cannot normally prevent her eggs from being eaten by other workers. Eggs are laid in open cells and police workers can recognize whether eggs are queen-laid or worker-laid, probably via chemical differences.

Worker policing is made possible because police workers have reliable information about who laid the eggs. In rare cases, such as in anarchistic honeybees [24] and the parasitic strain of the Cape honeybee [25], information about egg maternity is unreliable and, as a result, policing is ineffective. In cooperative breeders, the dominant female often kills the young of subordinates. As in the honeybee, reliable information is essential. In the dwarf mongoose, subordinate females do breed but normally their pregnancies are either not carried to term or the young disappear on the day of birth, presumably because they are killed by the dominant breeder [16]. Dwarf mongoose subordinates can only successfully breed when their pregnancy is synchronized with that of the dominant

female [16] suggesting that this makes it difficult for the dominant to distinguish between her own young and those of the subordinate. This strategy of 'cue scrambling' is also used by ant workers, who sometimes hide their eggs in the egg pile, thereby mixing the egg odors, which in turn prevents the removal of their eggs [26].

When does the individual win?

Bird-helpers can have power over the dominant breeder because it is difficult to recognize the maternity of an egg. If the dominant breeder cannot tell which eggs are hers, then she should not destroy them. When females can recognize their own eggs, as in the ostrich *Struthio camelis* and the Australian reed warbler *Acrocephalus australis*, they can expel eggs laid by other females [27,28]. Even if a female cannot distinguish between her own and another female's egg, she could use the presence of an egg before laying her own as a cue that that egg must have been laid by another bird. Acorn woodpeckers usually remove eggs already present in the nest when they themselves have not begun laying. This synchronizes reproduction, but only after what can become an extended period of reciprocal egg-destruction [29].

Under special conditions, the dominant can be in control without even having to exert power; for example, when the need for inbreeding avoidance limits the opportunities for subordinates to mate. When inbreeding is deleterious and the group comprises close relatives, subordinates should not mate with the dominant individual [30]. With no other mating opportunities available, monopolizing breeding is an easy victory for the dominant individual(s) [8,31,32].

In social insects, workers often benefit from a female-biased sex ratio [6] and will attempt to bias the sex ratio by killing males or investing more in young queens. How can the mother queen exert power over brood rearing, especially when the larvae are fed by workers? One possibility is for the queen to lay only male eggs during the period in which sexual offspring are reared, so the workers cannot cause female bias [33]. Brood of social Hymenoptera are usually considered to be powerless, because they are fed by adult workers and, therefore, cannot manipulate their food intake. Hence, a female larva cannot determine her own caste fate (i.e. whether she develops into a queen or a worker) (Box 4), because, to develop into a queen, a larva normally needs to be fed more. But when queens and workers are of the same size, as in *Melipona* bees, or when female brood can increase their own food intake by stealing food from a neighboring cell, as in some trigonine bees, they can have considerable power over their own fate and can develop into queens [34,35].

Combining theory with power

Our main aim here has been to promote the idea that a better insight into the reproductive characteristics of social groups will come about by combining theoretical predictions with a deeper understanding of the mechanisms that underlie the balance of power among conflicting parties. Inclusive fitness theory tells us that honeybee workers benefit by rearing the queen's sons rather than workers' sons. But, at the same time, inclusive fitness

Box 4. Control over own destiny

What determines whether one can choose one's own destiny, for example, whether a bee larva becomes a queen or a worker, or whether a subordinate African wild dog female can raise her own litter?

Social Hymenoptera

In most social Hymenoptera with queen-worker dimorphism, caste differentiation depends on differential feeding by workers, with queen larvae normally being given more food. Food control means that adult workers should have more power over the caste fate of the brood, who are relatively powerless because they are normally unable to influence their food intake, being legless and often segregated in individual cells, as in most social bees and wasps. The potential pay-off for being able to influence one's own caste-fate is substantial because an individual female larva can increase her fitness by developing into a queen instead of a worker. This is because any female is more related to her own offspring than she is to her sister's offspring [7,46]. In honeybees, the power struggle is won by workers who feed the brood progressively and rear queens in special, open, cells on special food (Fig. 1a). As a result, only 0.02% of female larvae become new queens, because queens are only reared when needed. By contrast, 5–20% of female *Melipona* stingless bee larvae become queens (Fig. 1b). What causes this difference? As in honeybees, workers build and provision the cells. But, in stingless bees, these cells are provided with a food mass that is sufficient for a larva to develop before the queen lays her egg in the cell. After laying, the cell is sealed. Hence, there is no interaction between adult workers and brood during larval development and workers cannot regulate which larvae are destined to become queens. In *Melipona*, queens and workers are reared in exactly the same cells and queens are the same size as the workers and can therefore develop on the same amount of food. This gives female brood power over their own caste-fate because they have access to food and female larvae can 'choose' to become a queen or a worker [7].

African wild dogs

Although worker/subordinate versus breeder caste is not fixed permanently in any social vertebrate, individuals are often constrained from breeding, as in African wild dogs *Lycaon pictus*. African wild dogs live in packs and defend large territories in which they hunt. Pups that are too young to join the hunt are left behind in the den, guarded by a babysitter, often the mother, whose presence is essential as predator protection [13]. The pack normally does not return to the same place after hunting unless they have pups. When a subordinate has given birth and is babysitting her young, the dominant female, who controls pack

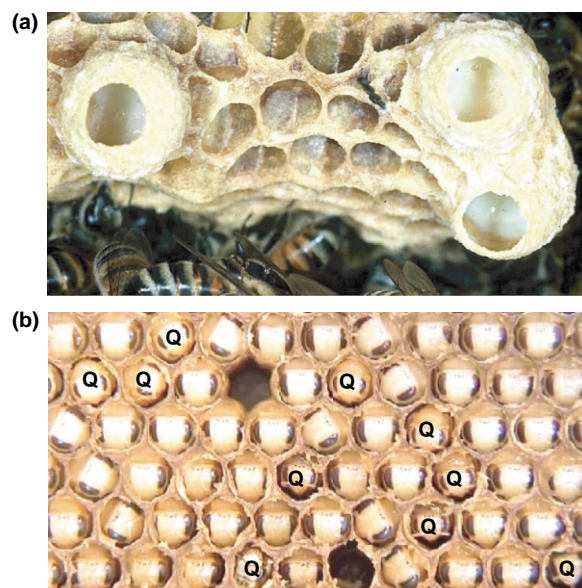


Fig. 1. Who becomes a queen? (a) Honeybee queen cells. Queens are reared in large, open cells constructed by workers. Workers only build queen cells when either the old queen has to be replaced, or during reproduction when the old colony divides into two or more new colonies each headed by one queen. Honeybee queens are much larger than workers and therefore need to be fed more and food of royal quality, royal jelly. Workers feed the larvae progressively. Therefore, larvae have no other choice than to wait in their cell until they are being fed by their sister-workers. (b) Part of the brood comb of *Melipona* stingless bees. The cell cappings have been removed to show the developing female pupae within the cells. Pupae marked 'Q' are queens, the others workers. Reproduced with permission from F.L.W. Ratnieks (a) and T. Wenseleers (b).

movement, can simply decide not to return to the den after hunting. African wild dogs are very reluctant to become isolated from their pack, because pack size determines hunting success, successful defence of territory, survival and reproduction [47]. This leaves the subordinate with a difficult choice, abandon her young and let them die, or stay with them and almost certainly die herself.

theory predicts that individual workers should produce their own sons if they can, even though this is counter to the interest of the other workers and the queen. But, because police workers can distinguish between worker- and queen-laid eggs, the optimum of the workers collectively and the queen is achieved rather than the optimum of the individual worker. This is an interesting case because the power to control individual worker reproduction is only possible because two parties, the queen and the workers collectively, cooperate. Each party individually would be unable to prevent individual workers from producing males. Effective policing of worker reproduction comes about only because the queen marks her eggs and the workers can discriminate between eggs laid by workers and the queen. In other cases, the costs and benefits of manipulative acts must be known to understand the balance of power. A subordinate individual should replace the same-sex dominant when that position becomes available, but this does not always happen. In the acorn woodpecker, reproductive vacancies are filled by unrelated individuals, often resulting in the same-sex

helper leaving the group [31]. The most important mechanism preventing same-sex helpers from filling the breeding vacancy is incest avoidance. However, this is not a general mechanism in birds [36,37] and so the full costs and benefits of reproductive decisions in the acorn woodpecker must be studied to understand the mechanisms that regulate replacement of dominant breeders.

In drawing attention to power, our primary aim has been to focus on a way of looking at reproductive conflicts and to encourage other researchers to look at their study species from the power perspective. Although such an approach is not new, it has seldom been made explicit in the past, and has never been the focus of systematic analysis. In this respect, the 'power' approach should be seen more as a new way of looking at things, rather than a new theory that makes predictions that can be tested. We have attempted to determine some general principles concerning the mechanisms that give one party power over others. Will it ever be possible to develop a 'theory of power' as we identify more general principles? Some of the general principles might be a suitable base for theory but,

as we have pointed out, idiosyncratic details of the biology of particular taxa are often of key importance. It is not clear whether a general theory can be based on a collection of special cases, each found in certain taxa.

In short, a fuller understanding of reproduction in social groups is a quintessentially biological problem, one that requires a synthesis of detail and diversity with theory and general principles, and in which theoreticians, field biologists and others can and must all play their part.

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